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A NEW CROCODILIAN FROM THE *NOTOSTYLOPS* BEDS OF PATAGONIA.[1]

By George Gaylord Simpson

The Scarritt Patagonian Expedition found remains of crocodiles, for the most part fragmentary, at a number of localities and horizons in Patagonia. Much of this material has not yet been prepared and its final publication must be long deferred, but there is already available a good, identifiable specimen from the *Notostylops* Beds which is of such interest that a preliminary discussion of it is here presented. This form, representing a new genus and species, is of unusual importance not only in itself and as a member of an extraordinarily rich and varied fauna, but also in its bearing on important problems of phylogeny, of paleogeography and faunal origin, and of correlation.

DESCRIPTION

Eocaiman, new genus

Type.—*Eocaiman cavernensis*, new species.

Distribution.—*Notostylops* Beds of Patagonia.

Diagnosis.—A true crocodilid or alligatorid with broad snout and alligatoroid bite. Pre- and inter-orbital crests as in *Jacaré*. Orbits large and close together. Anterior processes of palatines extending well in advance of posterior palatal vacuities and irregularly quadrate, as in *Caiman* but less elongate. Posterior palatal vacuities relatively wide and short, irregularly oval, the pterygoids forming the whole posterior border. Pterygoids short, and internal nares nearer their anterior than their posterior edges, relatively far forward. Lower jaw shallow but stout, with pronounced undulation of dental border. Symphysis extending about to fifth or sixth tooth, very shallow and wide. Splenial nearly reaching but not entering into symphysis. About fourteen maxillary and nineteen or possibly twenty dentary teeth. Fourth (?) maxillary and fourth and thirteenth dentary teeth much enlarged, the two latter each received in prominent pits in the palate. Posterior teeth pointed and crested, but with relatively depressed and blunt crowns.

Eocaiman cavernensis,[2] new species

Type.—Amer. Mus. No. 3158. Most of the front parts of skull and jaws. Found by G. G. Simpson and J. Hernández.

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[1] Publications of the Scarritt Patagonian Expedition, No. 14.

[2] The type was found in a cave, in a block fallen from the ceiling.

HORIZON AND LOCALITY.—*Notostylops* Beds, south of Lago Colhué-Huapí, Chubut, Argentina.

DIAGNOSIS.—Sole known species of the genus, as defined above and described below.

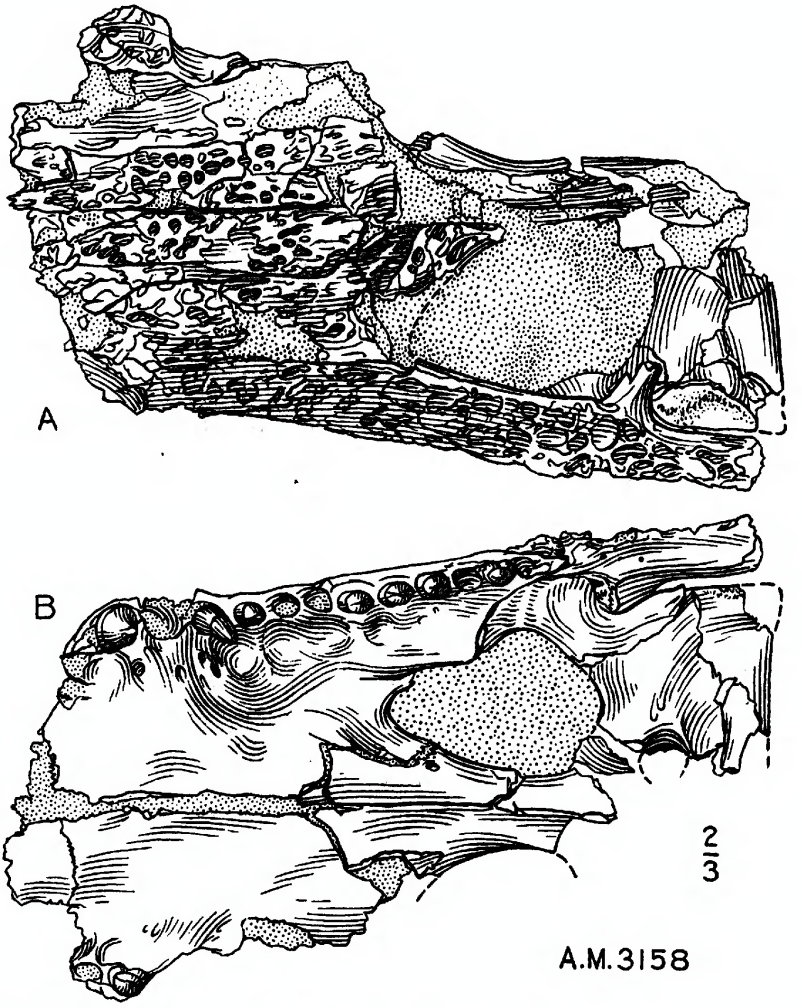

Fig. 1. *Eocaiman cavernensis*, new genus and species.

Type, Amer. Mus. No. 3158. Part of Skull. A, dorsal, view. B, palatal view. Two-thirds natural size. Drawn by John Germann.

The general contour of the preserved parts is much as in the living yacarés. The orbits, not completely preserved, were clearly very large and unusually long, with the base of the postorbital bar about 35 mm. posterior to the anterior orbital rim. This length is also correlated with relatively long and slender anterior or suborbital portion of the jugal.

The tip of the snout, with the external nares and the greater part of the premaxillae, is missing, and the remainder of the face is so much cracked that no details of interest are observed except that there was probably an antorbital ridge and that there is surely a strong semicircular crest between the anterior ends of the orbits as in *Jacaré*.

On the palate, the premaxillo-maxillary suture is nearly transverse in the middle portion, but was doubtless more oblique in the missing

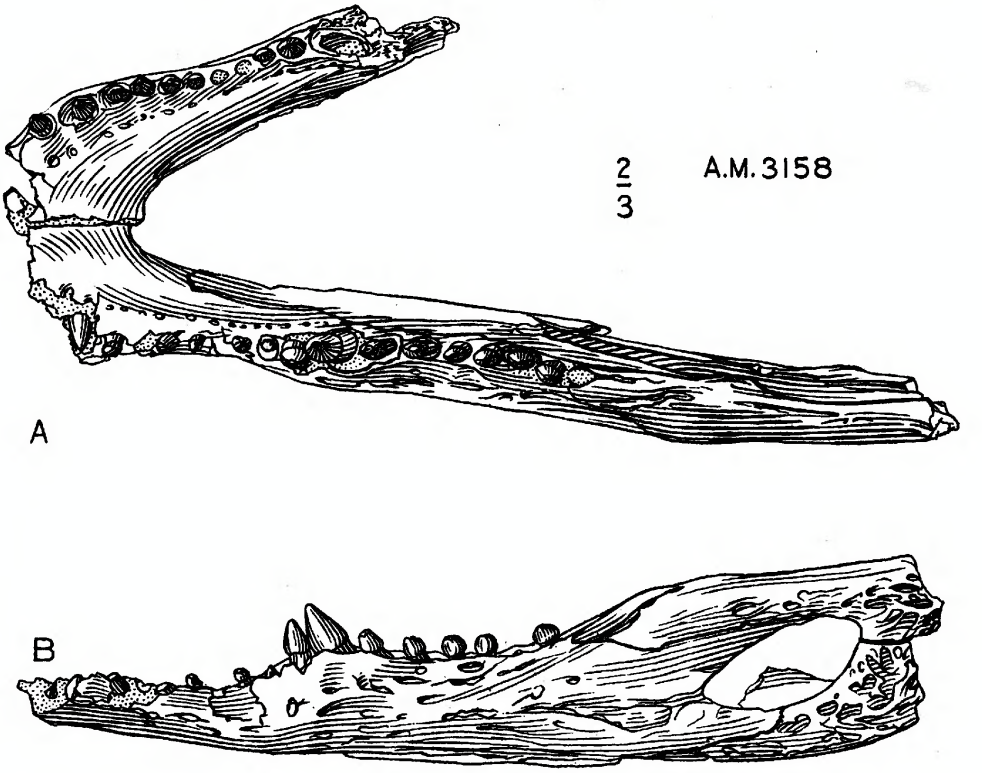

Fig. 2. *Eocaiman cavernensis*, new genus and species.
Type, Amer. Mus. No. 3158. Lower jaw. A, superior view. B, left lateral view. Two-thirds natural size. Drawn by John Germann.

outer parts. The palatine processes of the maxillae are marked by a very deep and prominent rugose pit internal to the fifth to eighth maxillary teeth. The anterior processes of the palatines are irregularly quadrate and extend about 20 mm. beyond the most posterior part of the palato-maxillary suture and about 12 or 13 mm. beyond the anterior end of the posterior palatal vacuities. The latter are about 22 mm. in width and 39 mm. in length and are almost of regular oval contour except for a

projection of the rim at the maxillo-ectopterygoid suture. At the posterior rim, in contrast to yacarés and many other recent crocodilians, the ectopterygoid and palatine are widely separated, so that this rim is formed almost exclusively by the pterygoid. The distance from the external rim to the tooth row is unusually great. The internal narial aperture was more anterior than in modern crocodilians, being closer to the palatal vacuity than to the posterior edge of the pterygoid plates. There were posterolateral crests on the pterygoid at the narial rims.

The lower jaw is remarkably shallow, but stout transversely. The anterior end is broken, so that it is impossible to ascertain whether it had a median projection or point, but it very possibly did, as the first tooth seems to have been large. The symphysis, extending to about the fifth or sixth tooth, is very wide, flat, and shallow. As shown by its sutures, the splenial nearly reached the symphysis but was not involved in it, much as in *Jacaré*, and the arrangement of the other elements, so far as preserved, is likewise almost exactly as in *Jacaré*. The external foramen is rather large, moderately elongate, with the surangular forming about the posterior third of its upper rim. The dental border rises at the fourth and thirteenth teeth (perhaps also at the first) and posterior to the teeth and sinks between these points, giving it a markedly irregular contour. Anterior to the thirteenth, the teeth are planted along the outer edge of the dental border and even point somewhat externally. The dental border posterior to the thirteenth tooth is depressed and widened, with the teeth near the midline, and there is a tendency to form a small horizontal flange at the upper edge of the splenial internal to the posterior teeth.

The premaxillary teeth are not known. There were probably fourteen maxillary teeth. In numbering them, the very probable assumption is made that there was one more tooth anterior to the thirteen of which crowns or alveoli are definitely visible. The third is a large tooth, considerably larger than the second, and the fourth is still larger, distinctly the largest maxillary tooth. The crown of the third is high, somewhat recurved, and crested. The fifth and sixth teeth are progressively much smaller, the seventh about the size of the sixth, the eighth larger and the subsequent teeth of about the same size until the somewhat smaller thirteenth and fourteenth. At least the ninth to thirteenth have low and bluntly pointed crowns, but laterally compressed and with distinct anteroposterior crests.

There is definite evidence of seventeen lower teeth and it is practically certain that broken bases of alveoli represent two more anterior

to these. Posterior to the definitely visible series is a depression possibly representing another tooth, although this is very uncertain and improbable. There were nineteen or possibly twenty lower teeth. The first was probably enlarged, but this is not wholly certain. The fourth is certainly enlarged and forms a "canine." The fifth is abruptly smaller and they then decrease in size to the ninth or tenth, becoming tiny, pointed but almost spatulate teeth. The eleventh is slightly and the twelfth much larger, while the thirteenth is the largest tooth in the lower jaw (with the improbable exception of the first), apparently even larger than the fourth. The fourteenth is abruptly smaller and the others still smaller and subequal, somewhat smaller and more depressed than the opposite teeth of the upper jaw.

AFFINITIES

A number of fossil crocodiles have been described from South America, but these are almost all of quite different ages from *Eocaiman* and either obviously distinct or so close to living forms as to require no special consideration here.

In 1896, however, Smith Woodward described two crocodiles sometimes considered as of early Tertiary age. These, *Notosuchus* and *Cynodontosuchus*, were listed as from the "red sandstones of . . . Neuquén." The confusion often existing in early collections makes the age uncertain, but the bulk of the material so labeled is surely Cretaceous, and as these genera are themselves of Cretaceous, even early Cretaceous, affinities, the presumption is that they, too, are Mesozoic and not Cenozoic in age. *Notosuchus* was referred to the Goniopholidae. Ameghino (1906, pp. 93–94) reported that *Notosuchus* occurs in some abundance, although always isolated (fragmentary) in the *Notostylops* Beds and in the coastal deposits of the marine Salamanca Formation. This was cited as another proof of the antiquity of the *Notostylops* Beds and their contemporaneity with the Salamanca.

Eocaiman is apparently the common crocodile in the *Notostylops* Beds, and it was probably on fragments of it that Ameghino based his assertion that *Notosuchus* occurs there. It is therefore necessary to compare the two. Fragments could readily be confused, but the good material now available shows that they are very distinct and cannot even have been at all closely related. Among the many differences of *Eocaiman* from *Notosuchus* are the following:

No antorbital vacuity.
Lower jaw more elongate and shallow.
Splenials excluded from symphysis.

Lateral vacuity of mandible smaller and less elongate.
Teeth much more numerous (about twice as many), and differently developed.
Nares (probably both external and internal) more typically crocodilid in structure.

These and many minor differences in the rather few known comparable characters show that the genera are profoundly distinct and have nothing to do with each other, probably not even belonging to the same broad family.

Ameghino's objective evidence for the occurrence of *Notosuchus* in the Salamanca Formation and in the *Notostylops* Beds consists chiefly of the specimens figured by him in 1906, Fig. 21. He did not give their stratigraphic or geographic origin, but the specimens are preserved in the Museo Nacional. The originals of Fig. 21*c*, *d*, *e*, *m*, *n*, *o*, and *u*, together with an unfigured fragment, are catalogued as No. 10881 and have Ameghino's label "Pico Salamanca. Salamanquense." They are therefore from the Salamanca Formation. Although really unidentifiable, there would be nothing remarkable in their belonging to *Notosuchus* as they are from well down in the Cretaceous. The original of Fig. 21*a* and *b* is No. 10885 and has conflicting labels. One, not clearly legible, appears to say "Río Chico—en el bajo al oeste [possibly another illegible word follows]—form. [formación?] *Notostylops*. Cocodrilo [?]," and the other says "*Notosuchus terrestris* Pico Salamanca." This single tooth may or may not be from the *Notostylops* Beds, and in any event is not identifiable. It might belong to *Eocaiman*, and there is no good reason for referring it to *Notosuchus* or for considering it the same as the Salamanca crocodile.

Comparison with *Cynodontosuchus* is unnecessary, as that is obviously a long-snouted crocodiloid form very unlike *Eocaiman*.

Among South American crocodiles, none of the known fossils is as close to *Eocaiman* as are the living *Jacaré* and *Caiman*.

In North America, the late Cretaceous (Hell Creek) *Brachychampsa* resembles *Eocaiman* in general form, but the tooth differentiation and some osteological features oppose close relationship. Comparable parts are too few for certainty, but it is conceivable that *Brachychampsa* and *Eocaiman*, while very distinct genera, did have a common ancestry.

Comparison with *Allognathosuchus* of the North American Paleocene and Eocene[1] is of unusual interest. The two are manifestly closely related. The general shape and proportions are similar. The palato-

[1]And possibly Oligocene, but, as noted by its author, *Allognathosuchus riggsi* Patterson, 1931, is not a typical member of the genus, and I suspect that it is closer to "*Crocodilus*" *prenasalis* Loomis, which Mook (1932) now refers to *Alligator*.

maxillary and premaxillo-maxillary sutures are nearly the same as far as visible. The posterior palatal vacuities are similarly bounded. The posterior nares occupy about the same position. The symphysis of the mandible is similarly wide and depressed. The peculiar wavy contour of the dental border is almost the same in both, and the shallow, thick dentaries are similar. In both, but, like some other resemblances, in unequal degree, the dental border is flattened and widened and a flange tends to develop internal to the posterior teeth. Except for the anterior end of the splenial, the shape and arrangement of the known mandibular elements are almost the same. The number of teeth is the same or very nearly so, and their differentiation and relative sizes are almost identical in the two genera.

The differences, while of generic value, are not profound. In *Eocaiman* the symphysis was probably slightly shallower and wider. The thickness of the dentary and the development of a dental shelf are not quite so pronounced; the splenial does not distinctly enter the symphysis; the lateral vacuity is relatively slightly larger and more elongate. The posterior palatal vacuities are larger. The anterior ends of the jugal, and probably some other skull elements, are more slender; in fact, the construction throughout is somewhat lighter and less massive, doubtless an adaptive feature of no great significance. The posterior teeth, while rather blunt, fall considerably short of the extreme specialization of *Allognathosuchus* in this respect.

In the development of the posterior teeth and the probably correlated lighter construction of skull and jaws, *Alligator prenasalis* is closer to *Eocaiman* than is *Allognathosuchus*. Yet this Oligocene North American species retains the splenial symphysis and some other minor characters of *Allognathosuchus* already lost or modified in *Eocaiman*. It does not have the pre- and interorbital ridges already present in *Eocaiman*. In many respects, *Alligator prenasalis*, which is a very early and primitive *Alligator* unlike *A. mississippiensis* in many important characters, is more like *Allognathosuchus*, *Eocaiman*, and *Caiman* or *Jacaré* than are the living alligators. But it does appear to be advancing toward typical *Alligator*, and these resemblances are doubtless due to its being less removed from the point of separation of these related phyla.

Caimanoidea Mehl, 1916, was considered by its author to be especially, but collaterally, related to *Caiman*. Reconsideration with the much better data of several sorts now available suggests that *Caimanoidea* is not particularly related to *Caiman* but is nearer the *Alligator* phylum. Details of structure are not very clearly known, but particu-

larly in its less developed and somewhat different dental differentiation, it is even farther from *Eocaiman* than is its contemporary *Alligator prenasalis*.[1]

Among living forms, *Eocaiman* surely most resembles *Jacaré* and *Caiman*, or *Caiman* sensu lato. In some respects, such as the slope of the palato-maxillary suture, it is more *Caiman*-like; in others, such as the less elongate snout and prominent interorbital crest, more *Jacaré*-like. In still others, apparently primitive, such as the large participation of the pterygoid in the rim of the posterior palatal vacuity or the more anterior position of the internal nares, it differs from both. In the known parts there seems nothing to exclude *Eocaiman* from the ancestry of both *Jacaré* and *Caiman*.[2]

CONCLUSIONS

1. *Eocaiman cavernensis* is a new and distinctive alligatoroid form from the *Notostylops* Beds, probably Eocene, of Patagonia.

2. It is apparently the common crocodile of those beds, and is surely very distinct from *Notosuchus*. Contrary to Ameghino, there is no evidence that *Notosuchus* occurs in the *Notostylops* Beds. To that extent, his belief in the antiquity of that formation is thus still further weakened.

3. So far as may be judged on still too scanty evidence, *Eocaiman* is of early Tertiary, probably Eocene, aspect as regards evolutionary advance.

4. *Eocaiman* seems to stand near the ancestry of *Caiman* and *Jacaré*, suggesting that those genera have developed in South America during the Tertiary, and probably independent of other connections since early in or even before that period.

6. Its further apparent relationship with *Allognathosuchus* and with other North American early Tertiary forms strongly suggests that these North and South American alligatoroid genera are a distinctive group of common geographic and zoölogic origin.

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[1] I formerly (1930) suggested that *Caimanoidea*, while not a direct ancestor, was nearer to *Alligator* than to *Caiman* and was also nearer the alligator main line than was *Allognathosuchus*. Patterson (1931) somewhat misunderstood me in believing that I did not regard *Allognathosuchus* as closely related to *Alligator*—the intention was only to show it as less close than *Caimanoidea*. I agree with him in supposing *Allognathosuchus* a fair structural ancestor of *Alligator*, especially if *Allognathosuchus riggsi* belongs in that genus, which is, however, rather questionable. But the typical species of *Allognathosuchus* were surely aberrant in dentition and accompanying specializations. The better knowledge since given by Mook (1932) of *Alligator prenasalis*, as old as *Caimanoidea* or *?Allognathosuchus riggsi*, also alters the conception of these phylogenetic details. In any event, all these forms represent more or less diverse but closely related branches of a distinctive alligatoroid group.

[2] One possible distinction is that in the living forms it is normally the twelfth and in *Eocaiman* the thirteenth lower tooth which is enlarged, but the exact number of teeth is variable, and this slight transposition is not a real obstacle to close relationship.

6. This significantly adds to the evidence for a faunal and geographic connection between North and South America near or somewhat before the beginning of the Tertiary.

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